DIVISION OF PARENTAL ROLES IN THE MONOGAMOUS WESTERN SANDPIPER, *Calidris mauri*

By

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A

THESIS

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Abstract. I investigated whether male and female Western Sandpipers (*Calidris mauri*) contributed equal amounts of parental care during the breeding season, near Nome, AK, USA (64° N) during 1998 and 1999. I repeatedly observed which parent was present at the nest during incubation and which parent tended the brood during the brood care period. Females incubated predominantly at night (18:00 - 06:00 hr ADT); males incubated predominantly during the day (06:00 - 18:00 hr ADT). Males spent more time incubating than females (57% vs. 43%, $P < 0.05$). Females deserted their broods on average 5.6 days after hatch, while males tended broods on average 13.0 days after hatch ($P < 0.001$). Nests that hatched earlier in the season received significantly more bi-parental care during the brood care period ($P = 0.01$). Timing of nest initiation had the greatest effect on the division of parental care between sexes for Western Sandpipers.

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GENERAL INTRODUCTION

Males and females must come together in order to breed, and to some extent, they must cooperate to be successful. Both sexes, however, are under selection to maximize their individual lifetime reproductive success (Williams 1966). Thus, the interests of each sex may be in conflict, because each individual may gain by investing less in current offspring than its mate (Dawkins 1976). In birds, parental care includes defense and incubation of eggs, as well as brooding and defense of the young. Such care can be performed by either sex. The division of parental care between the sexes varies within and among species and may be closely related to mating behavior (Clutton-Brock 1991, Liker and Szekely 1999).

Shorebirds (Scolopacidae) exhibit exceptional diversity of mating and parental behavior traits, making them excellent subjects to investigate adaptive explanations for parental care patterns (Erckmann 1983, Szekely and Williams 1995, Amat et al. 2000). In this study, I investigated the division of parental roles for breeding Western Sandpipers (*Calidris mauri*) during the incubation and brood care period.

Incubation may be the most confining of parental-care behaviors because it consumes time and cannot be postponed (Ketterson and Nolan 1994). Thus, incubation may come at a cost of lost mating or foraging opportunities. Sandpipers use multiple incubation strategies, and those strategies vary within and among mating systems (Miller 1985, Brunton 1988, Pierce 1997). Within a monogamous mating system, where incubation is shared, there is considerable variation in daily pattern of incubation duties. Some species, such as the Least Sandpiper (*Calidris minutilla*) and Dunlin (*C. alpina*),

exhibit male-dominated incubation effort, with females providing only nocturnal incubation (Miller 1985, Jonsson 1987). These species contrast to the Semipalmated Sandpiper (*C. pusilla*), which exhibits temporally variable patterns of shared incubation (Ashkenazie and Safriel 1979). Clear differences exist in incubation duties between sexes among sandpipers (Ashkenazie and Safriel 1979, Bergstrom 1988, Brunton 1988, Pierce 1997). Nonetheless, few studies have attempted to explain the daily incubation pattern exhibited by monogamous shorebirds. In Chapter I, I quantify the pattern of incubation between the sexes for Western Sandpipers and evaluate the following hypotheses proposed to explain this pattern of incubation: (1) females may recover energy spent on eggs most efficiently if males incubate when food is most available, allowing females to feed at those times (female condition hypothesis, Miller 1977); and (2) temporal differences between the sexes in incubation duties yield unequal effort per unit time (differential cost of nocturnal incubation hypothesis, Miller 1977).

Optional uniparental brood desertion by either parent following hatch is common among shorebirds (Ashkenazie and Safriel 1979, Gratto-Trevor 1991, Miller 1985, Pierce 1997). For most *Calidris* species, females are more likely than males to desert their brood shortly after hatch. The reasons for female desertion among monogamous bird species are not clearly understood, and evidence for costs and benefits to either sex is scant (Clutton-Brock 1991). Several hypotheses have been formulated to account for offspring desertion (Erckmann 1983, Szekely 1996, Amat et al. 1999). These hypotheses include: (1) energetic limitation imposed on breeding females by the costs of reproduction (differential parental capacity; Ashkenazie and Safriel 1979, Erckmann

1981, Pierce 1997); (2) increased female survival (Ashkenazie and Safriel 1979, Myers 1981, Gratto-Trevor 1991); and (3) increased opportunity to acquire new matings within the same breeding season (remating opportunity hypothesis; Szekely et al. 1999). In chapter II, I examine the timing of female brood desertion by Western Sandpipers and evaluate hypotheses proposed to explain offspring desertion for single-clutch arctic nesting shorebirds.

The Western Sandpiper is a small migratory shorebird that breeds in coastal Alaska and far eastern Siberia. During the non-breeding season, adults and juvenals migrate south, wintering from Northern California to Peru (Wilson 1994). Western Sandpipers are sexually monomorphic in plumage, but females are larger (Wilson 1994). Biparental incubation is obligate (Erckmann 1981) throughout the 21-day incubation period (Holmes 1972). Females lay a fixed clutch of 4 eggs (Sandercock 1997). Chicks are precocial, leave the nest within 24 hr of hatching, and are never fed by their parents (Holmes 1972). Western Sandpipers are primarily monogamous and raise only one brood per season, but renesting may follow failure at an early breeding stage (Holmes 1972, Sandercock 1997). During the brood care period parents protect and brood chicks periodically for the first 1-2 weeks and lead them to feeding areas. Young can fly from 15 to 35 days after hatching (Harrison 1978). All Scolopacidae young are precocial and feed themselves shortly after hatch.

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CHAPTER 1. PARENTAL DIFFERENCES IN THE DAILY INCUBATION PATTERN OF WESTERN SANDPIPERS[1]

Abstract. Considerable interspecific variation exists in the division of incubation effort between sexes within the Scolopacidae. Two hypotheses have been proposed to explain those differences: (1) limited energy reserves in females; (2) differential cost of nocturnal incubation. I investigated whether male and female Western Sandpipers (*Calidris mauri*) contributed equal amounts of parental care during the breeding season near Nome, AK (64° N) during 1999. I repeatedly observed which parent was present at the nest during the incubation period. Data were collected for 33 mated pairs, 23 of which successfully hatched eggs. Females incubated mostly at night (18:00 - 06:00 hr ADT); males incubated mostly during the day (06:00 - 18:00 hr ADT). That daily pattern of incubation was constant throughout the incubation period ($P = 0.6$). Males, however, spent more time incubating than females (57% vs. 43%, $P < 0.05$). Nests that hatched later in the season received more incubation effort by males ($F = 4.32$, $P = 0.06$). Results provide evidence consistent with the hypothesis that low energy reserves in females favor incubation by both sexes.

Key words: *Calidris mauri*, incubation, parental care, parental roles, Western Sandpiper.

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[1]Prepared for submission in Condor.

INTRODUCTION

Shorebirds show a variety of parental-care strategies. Consequently, these birds have been the focus of many studies investigating selective forces influencing the evolution of mating systems (Pierce 1997, Borowik and McLennan 1999). The division of parental care including incubating and guarding eggs, brooding, and defending chicks, is thought to influence mating system because the costs of parental care limit opportunities for future matings (Erckmann 1983). Parental care can vary from exclusive care by either sex to equally shared biparental care. Even among biparental birds, both parents may divide care in a variety of ways (Clutton-Brock 1991, Liker 1999). Shorebirds (Charadrii) exhibit the greatest array of parental care among birds. For shorebirds, the sandpipers (Scolopacidae) show most major types of mating systems, including monogamy, polygyny, and polyandry (Erckmann 1981).

Incubation may be the most confining of parental-care behaviors because it consumes time and cannot be postponed (Ketterson and Nolan 1994). Thus, incubation may come at a cost of lost mating or foraging opportunities. Sandpipers use multiple incubation strategies, and those strategies vary within and among mating systems (Miller 1985, Brunton 1988, Pierce 1997). Within a monogamous mating system, where incubation is shared, there is considerable variation in daily pattern of incubation duties. Some species, such as the Least Sandpiper (*Calidris minutilla*) and Dunlin (*C. alpina*), exhibit male-dominated incubation effort, with females providing only nocturnal incubation (Miller 1985, Jonsson 1987). These species contrast to the Semipalmated Sandpiper (*C. pusilla*), which exhibits temporally variable patterns of shared incubation

(Ashkenazie and Safriel 1979). Clear differences exist in incubation duties between sexes among sandpipers (Ashkenazie and Safriel 1979, Bergstrom 1988, Brunton 1988, Pierce 1997). Nonetheless, few studies have attempted to explain the daily incubation pattern exhibited by monogamous shorebirds. Miller (1977) proposed two hypotheses to explain the pattern of incubation: (1) females may recover energy spent on eggs most efficiently if males incubate when food is most available, allowing females to feed at those times (**female condition hypothesis**); and (2) temporal differences between the sexes in incubation duties yield unequal effort per unit time (**differential cost of nocturnal incubation hypothesis**).

The female condition hypothesis assumes that females have reduced energetic reserves relative to males because of egg laying. As a consequence, females forage during the day because food availability is greater at that time (Miller 1977). Many studies report higher energetic costs in females relative to males during incubation (Ashkenazie and Safriel 1979, Erckmann 1981, Brunton 1988). For example, Erckmann (1981) conducted a field experiment where equal numbers of male and female Western Sandpipers were experimentally deserted by the opposite sex during incubation. All experimentally deserted sandpipers of both sexes abandoned their nests before eggs could hatch; however, the mean time from experimental desertion to nest abandonment was significantly shorter for females than males (4.2 vs. 7.8 days). Incubating females also lost mass more rapidly than males (Erckmann 1981).

Previous reports of limited energy reserves in breeding sandpipers suggest that different stages of the incubation period may yield different energetic costs for each sex

(Brunton 1988). Egg laying has caused initially large differences in energy investment between the sexes in Semipalmated Sandpipers (Ashkenazie and Safriel 1979, Brunton 1988) because egg-laying costs are exceeded by the costs of territorial defense by males (Ashkenazie and Safriel 1979). Differences in energy costs between male and female Killdeer (*Charadrius vociferous*) before the onset of incubation limit energy expenditure during later stages of incubation, indicating the cost of egg production influences strategies of parental care exhibited by females (Brunton 1988). Other studies indicate weather and predation play a large role in determining differences in daily energy expenditure between sexes (Piersma and Morrison 1994, Brunton 1988).

The **differential cost of nocturnal incubation hypothesis** suggests larger individuals are more efficient incubators and thus provide nocturnal incubation (Miller 1977). This hypothesis is based on the assumption that energetic costs of incubation differ between night and day. Despite the general belief (e.g., Remmert 1980) that sub-arctic and arctic conditions during the breeding season are relatively constant, presumably because of near 24 hr daylight, diurnal patterns exist for several climatic variables (Piersma and Morrison 1994). Both solar irradiance and air temperature fluctuated diurnally during June and July at 69° N. Nighttime temperatures were significantly cooler than daytime temperatures. Cloud cover had a strong influence on ground-surface temperature. Thus, nighttime incubators are exposed to cooler conditions and likely experience higher energetic costs relative to daytime incubators.

Body size influences the energetic costs of incubation (Ricklefs 1974, Jonsson and Alerstam 1990). Energy requirements for most activities increase with increasing

body size; however, larger body mass also increases energy storing capacity. Snyder and Wiley (1976) suggest that larger individuals are able to cover and warm eggs more efficiently than smaller individuals. Measurements of metabolic rates of incubating sandpipers near Barrow, AK, indicate incubation involves rates of energy consumption 10-50% in excess of resting metabolic rates (Norton 1973). Most *Calidris* sandpipers exhibit reversed sexual size dimorphism. Phylogenetic comparisons of total incubation effort revealed differences in incubation effort between the sexes but did not explain the pattern of reversed sexual size dimorphism (Figuerola 1999). Figuerola (1999), however, did not consider nocturnal incubation. Body size may influence probability of nighttime incubation because larger individuals have lower mass specific metabolic rates (Norton 1973). Additionally, larger individuals have lower critical temperatures and respond metabolically less to changes in temperature than do small individuals (Norton 1973). If larger body size is more efficient at warming eggs, then the larger sex should incubate at night, during cooler temperatures.

In this study, I investigated the division of parental roles for breeding Western Sandpipers (*Calidris mauri*) during the incubation period. The Western Sandpiper is a small (25-28 g) migratory bird that breeds in coastal Alaska, and far eastern Siberia, Russia. During the nonbreeding season, adults and juvenals migrate south, wintering from Northern California, to Peru (Wilson 1994). Western Sandpipers are monomorphic in plumage, but females are 12% larger than males (Wilson 1994, Sandercock 1998a). Females lay a fixed clutch of 4 eggs (Sandercock 1997). Both sexes participate in incubation duties (Erckmann 1981) throughout the 21-day incubation period (Holmes

1972). Previous studies indicate incubation is divided equally between the sexes and that males provide most of the incubation effort during the day (Holmes 1971, Erckmann 1983). I examined two hypotheses explaining division of incubation effort in Western Sandpipers.

Hypothesis 1: female condition. Females may recover energy spent on eggs most efficiently if males incubate when food is most available, allowing females to feed at those times. If energy reserves are limited in females relative to males, then overall incubation effort is expected to be male biased (Erckmann 1983, Brunton 1988, Pierce 1997). If energy reserves are limited in females immediately following egg laying, they should provide relatively less parental effort during incubation. If females limit incubation effort as a result of reduced energy reserves, then timing of brood desertion should be a function of female body condition.

Hypothesis 2: differential cost of nocturnal incubation. Temporal differences in incubation duties between the sexes yield unequal effort per unit time. Based on body size differences (Sandercock 1998a) and the energetics of incubation (Jonsson and Alerstam 1990), I predicted female Western Sandpipers would disproportionately incubate at night and body size should be positively associated with nocturnal incubation effort. Furthermore, this pattern should hold true for all *Calidris* species exhibiting reversed sexual size dimorphism.

METHODS

STUDY AREA

I studied the division of parental roles in Western Sandpipers near Cape Nome (64°20'N, 164°56'W) on the southwest tip of the Seward Peninsula, 21 km east of Nome, AK, from May to July 1999. The 4-km^2 study area, located on the western edge of Safety Sound, consisted of a mosaic of low ridges and tundra ponds (Sandercock 1998b). The breeding biology of this population of Western Sandpipers has been studied since 1993 (Sandercock 1998b).

FIELD METHODS

I located nests by systematically walking the tundra and observing sandpipers that flushed or gave distraction displays (Sandercock 1998b). If I could not find the clutch immediately after the parent flushed, I observed the bird from ~ 25 m until it returned to the nest. Nests were marked with a line of 4 sticks and a short stake placed 10 m from the nest. I captured incubating birds using traps placed over the nest. Captured adults were given unique color band combinations and numbered metal bands. I attempted to capture both individuals attending a nest. Sex was determined using culmen length (<24.2 mm for male, >24.8 mm for female; Cartar 1984) and territorial or mating behavior. No overlap in culmen length between the sexes greatly reduced the possibility of misidentifying the sex of an individual. Exposed culmen length, tarsus length, and flattened wing chord were measured to the nearest 0.1 mm. I weighed adults and nestlings with a Pesola balance (± 0.5 g). I calculated index of body condition as the residuals from a regression of body mass on a multivariate measure of structural body size (PCI). Structural body size was estimated using principal component analysis. Body condition estimates were based on post-hatch measurements of body mass. Data

were collected in accordance with Institutional Animal Care and Use Committee guidelines at the University of Alaska Fairbanks.

I floated eggs in a small cup of warm water and determined stage of incubation based on egg buoyancy (Sandercock 1998b) to estimate stage of incubation if a nest already contained 4 eggs when located. Otherwise, clutch initiation and completion of laying were determined from egg-laying schedules and hatch date was estimated from the mean length of incubation (21 days) for Western Sandpipers (Sandercock 1998c). Nests were monitored until they failed (predation or desertion) or successfully hatched chicks. A successful nesting attempt was defined as having at least one chick hatch. Nesting pairs were divided into two categories: early and late nesters. I defined early nesters as pairs that initiated nesting before the median clutch initiation date. Data from nests that suffered predation or desertion (n = 7) were excluded from analyses.

SAMPLING PROCEDURE

I divided the 24-hr day into four periods (06:01-12:00, 12:01-18:00, 18:01-00:00, 00:01-06:00 Alaska Daylight Time, ADT). Prior observation of this population indicated adult incubation bouts are lengthy (6-12 hr, pers. obs.). By dividing the 24-hr day into four 6-hour periods, I reduced the likelihood of sampling the same individual more than once within a particular time period because individuals tend to incubate for 8 to 12 hr bouts. In this geographical region, night is centered on 03:20 ADT, and solar noon occurs at 15:20 ADT. The incubation period was divided into 3 weeklong periods following completion of the clutch: 1-7 days; 8-14 days; and 14-21 days. I attempted to sample equally across and within periods over the breeding season. To minimize disturbance, I

tried to examine nests no more than once a day to determine sex of incubating birds. If a nest was observed more than once per 24 hr (n = 9, 2.3%), that sample was included in the analysis only if the two observations fell into different time periods. Incubating birds flushed from eggs when observers approached. Color band combination of the flushed bird was identified and recorded; this procedure usually required < 1 min. In a few instances, an active nest was relocated without an incubating bird (n = 5, 1.3%); these samples were excluded from analyses.

STATISTICAL ANALYSES

Each nest was considered as the unit of analysis. To investigate the relationship between daytime and nighttime incubation effort by females, I used a paired sample t-test (SAS Institute, 2000). The proportion of female incubation was analyzed by an analysis of covariance (ANCOVA) in which early or late nest initiation was the factor and time of day was the covariate (Zar 1996). Normal approximation to the binomial test was used to compare proportion of incubation effort for males and females during each week of the 3-week incubation period. To determine effects of initiating a nesting attempt earlier or later than the median nest initiation date on incubation effort by each sex, I used a two-sample t-test (SAS Institute). I used a linear regression to test for incubation effort as a function of hatch date. I used principal component analysis to create an index of Western Sandpiper body size based on culmen and wing length using a correlation matrix (Rising and Somers 1989). Loadings for culmen and wing chord were positive in the first principal component, and this component explained 69.0% of the variation in body size. The proportion of female incubation effort in relation to body condition during

incubation was analyzed by an ANCOVA in which early or late nest initiation was the factor and body condition was the covariate. I used Pearson's correlation to test for an association between female incubation effort over four 6-hr periods and sun elevation. To determine if the proportion of female incubation effort over four 6-hr periods varied across the incubation period, I used a randomized-block analysis of variance on ranks with week as the blocks and time of day as the treatment (Friedman's test). All data were inspected for normality and homoscedasticity (Zar 1996). In all analyses, probability of committing a Type I error was set to $\alpha = 0.05$.

RESULTS

I obtained incubation data from 33 nests of Western Sandpipers, 7 of which were depredated and 3 abandoned. Twenty-three successful nesting attempts were initiated from 21 May to 9 June, and clutch size ranged from 3 to 4 eggs. Median date of clutch initiation for all nests ($n = 33$) and the 23 nests used to analyze division of incubation between sexes was 1 June. Within the 23 nests monitored to determine within-day pattern of incubation, females incubated mostly (61.7% of time) at night (18:00 hr-06:00 hr ADT), males mostly (68.1% of time) during the day (06:00 hr-18:00 hr ADT; $t = 3.21$, $P = 0.01$, $n = 14$ nests, 398 observations, Fig. 1.1). No difference occurred between early-nesting and late-nesting birds with respect to within-day pattern of incubation ($F_{1,12} = 1.11$, $P > 0.3$, $n = 23$ nests).

FEMALE CONDITION

Over the entire incubation period, males were recorded on nests significantly more frequently than females (57 % vs. 43 %; binomial test z = 2.762, $P < 0.01$, $n = 23$ nests). During week 1 of the incubation period, females were recorded on nests significantly less than males (36 % vs. 63 %; binomial test z = 2.762, $P < 0.01$, $n = 23$ nests, Fig. 1.2). I found a weak trend for males to decrease incubation effort in weeks 2 and 3, as females increased effort ($P = 0.06$, Fig 1.2). Early-nesting males and females provided similar incubation effort ($t = 0.61$, $P = 0.56$, $n = 9$), however, late-nesting females provided significantly less effort than males ($t = 2.25$, $P = 0.04$, $n = 13$, Fig. 1.3). Nests that hatched earlier in the season tended to receive more care by females than males during the incubation period ($F_{1,14} = 4.32$, $P = 0.06$, $R^2 = 0.25$, $n = 15$ nests, Fig. 1.4a,b). Female body condition during incubation was not associated with incubation effort ($F_{2,6} = 0.97$, $P = 0.4$, $n = 7$ nests, Fig. 1.5). Incubation data were collected equally between day and nighttime, and there was no effect of nest initiation date with respect to the association between total incubation effort and female body condition during incubation ($P = 0.3$)

DIFFERENTIAL COST OF NOCTURNAL INCUBATION

Daily pattern of incubation between sexes was correlated with sun elevation (degrees above the horizon; $r = 0.84$, $P = 0.01$, $n = 14$ nests, Fig. 1.6). A difference in the 24 hr incubation pattern over the three-week incubation period relative to either corrected day of incubation (i.e., days 1-21 of incubation; $F_{7,13} = 6.21$, $P = 0.6$, $n = 24$), or Julian date (i.e. June 3-24; $F_{7,25} = 3.22$, $P = 0.6$, $n = 40$) could not be detected. Considerable variation exists among pairs with respect to the pattern of daily incubation (Fig. 1.7).

DISCUSSION

DAILY PATTERN OF INCUBATION

Female Western Sandpipers incubated primarily at night and males incubated primarily during the day (Fig 1.1), similar to the Least Sandpiper and Dunlin (Cramp and Simmons 1983, Miller 1985). A similar, but weakly supported pattern, was reported for Baird's Sandpiper (*Calidris bairdii*, Miller 1985). Males have been reported to incubate predominantly during the day in other *Calidris* species (i.e. Little Stint, *Calidris minuta*, Knot, *C. canutus*), which may be an artifact of data collected principally during the day (Miller 1985). This pattern contrasts with the variable pattern of daily incubation displayed in monogamous Semipalmated and Purple sandpipers (*Calidris maritima*) (Ashkenazie and Safriel 1979, Pierce 1997). Overall, one of the most consistent patterns within Calidridines describes females as predominantly nocturnal incubators and males as mostly daytime incubators (Table 1.2).

FEMALE CONDITION

I observed male-biased incubation effort (59%, $P = 0.01$) throughout the 21 day period, which is common among *Calidris* species (i.e., Dunlin, Semipalmated, Least, and Purple sandpipers; Ashkenazie and Safriel 1979, Cramp and Simmons 1983, Miller 1985, Pierce 1997). Females contributed less effort during all stages of incubation, particularly the early period (Fig. 1.2). I observed a non-significant trend for females to increase effort over the incubation period ($P = 0.06$, Fig. 1.2). During early stages of incubation, females incubated only 36% of the time, increasing during mid and late stages to a maximum of 46%. Female Western Sandpipers provided less incubation effort,

especially immediately following egg laying. My findings are consistent with other reports that suggest females may be energetically limited as a result of egg laying (Ashkenazie and Safriel 1979, Brunton 1988). Increasing female effort over the incubation period, however, is not typical for most *Calidris* species (Table 1.1).

Total incubation effort by females was independent of body condition during incubation, indicating differences in energetic requirements between the sexes do not satisfactorily explain timing of female incubation effort. Ashkenazie and Safriel (1979) reported energetic costs from behavioral observations of breeding Semipalmated Sandpipers near Barrrow, AK, and reported considerable differences in the energetic costs of sex specific activities. Those authors determined that females had a relatively high energy deficit by the end of incubation. Methods described in that study, however (weight change as an indicator of energetic reserves), have been criticized because individuals may experience weight loss for reasons unrelated to changes in energy reserves (i.e., regression of reproductive organs; Ricklefs 1974). Using percentage of fat per fat-free weight as a measure of condition, Gratto-Trevor (1991) reported female Semipalmated Sandpipers had higher fat levels than males before incubation, and lower levels shortly before deserting the brood. My data, in conjunction with those studies, provide partial support for higher energetic costs for females relative to males. I did not find a direct relationship between body condition during incubation and total incubation effort by females, this may have been an artifact of temporal variation in data collection.

Early nesting is thought to confer a reproductive advantage in sandpipers (Soikkeli 1967, Daan et al. 1988). If reduced energy reserves limit incubation effort, then

early-nesting females should be capable of contributing more incubation effort because they are in better condition at the beginning and end of egg laying than later-nesting females. I documented that timing of clutch initiation influenced proportion of time each sex contributed towards incubation. Both early and late nesters exhibited male-biased incubation (Fig. 1.3) but females that nested earlier increased incubation effort relative to those nesting later (Fig. 1.4b). Early-nesting females are contributing more incubation effort. Data describing sex-specific incubation effort as a function of clutch initiation date for *Calidris* species are sparse.

An important corollary of the female condition hypothesis is that females feed during the day, when prey availability is greater. Prey availability was not measured during this study. Other studies suggested that sandpiper prey behavior availability is higher during the day (Erckmann 1981, Holmes 1971); however, a review of the literature provides conflicting evidence. Pienkowski (1983) reported intertidal invertebrates increased surface activity at warmer temperatures; indicating that prey availability may be higher during the day. In contrast, Dugan (1981) reported activity levels of *Corophium* may be higher at night and closer to the surface; thus some prey are potentially more available at night. Moreover, air temperature might influence rate of prey capture because feeding rate is limited by digestion rate, which is dependent on environmental temperatures (Klaaseen et al. 1990). Higher temperatures would then increase feeding rates, thereby making daytime foraging more efficient. Unfortunately, information describing diurnal behaviors of invertebrates in arctic coastal ponds (e.g., Chironomidae) is lacking. Furthermore, most data collected to describe sandpiper prey

behavior come from intertidal stopover sites during migration (Pienkowski 1983, Lifjeld 1984, McCurdy 1997, Sutherland et al. 2000). This lack of data makes it difficult to assess whether foraging is more profitable during daytime hours on the breeding grounds.

Changes in availability of invertebrates in response to increasing photoperiod (i.e. daily surface temperature) may shift daily foraging habits and, consequently, incubation pattern over time (i.e. June 1-30). My results indicate that Western Sandpipers do not shift the daily incubation pattern over the 3-week incubation period but females do incubate more during later stages of incubation. Evidence in support of the female condition hypothesis (Miller 1977) is incomplete. Females may experience decreased energy reserves, especially directly following egg laying but it is not clear whether foraging during the day provides females with a foraging advantage relative to males.

Other hypotheses proposed to explain differences in parental care strategies include the intraspecific niche differentiation hypothesis, which states that differences in habitat use may interact with parental care. Female Western Sandpiper bill length is 16% longer than males (Mueller 1989). This magnitude of a difference in bill morphology is predicted to be accompanied by specialization in diet, feeding behavior, or feeding habitat (Lack 1968). Consequently, spatial distribution of food availability may have a strong influence on the pattern of parental care exhibited by sandpipers (Pitelka et al. 1974, Pierce 1997). Most *Calidris* species obtain much of their food away from nesting territories (Ashkenazie and Safriel 1979, Holmes 1971). Reports of spatial segregation between the sexes while foraging exist; however, most data were collected during migration or at overwintering sites (Puttick 1981). Differences in foraging strategies

between the sexes may influence incubation timing and effort, since incubation duties limit foraging time. Female Western Sandpipers may not only be foraging in different areas, but also may be using different habitat types (pers. obs.). Anecdotal data indicate females travel longer distances (to a nearby estuary) to forage, while males are more likely to forage at the edge of freshwater ponds within 300 m of their nests. These observed foraging differences suggest males and females may be using different foraging strategies; optimal foraging strategies may differ by sex. Data describing forage differences between the sexes during the breeding season are sparse and deserve additional study.

DIFFERENTIAL COST OF NOCTURNAL INCUBATION

I found limited evidence in support of the differential cost of nocturnal incubation hypothesis. Indeed, female Western Sandpipers incubate predominantly at night (Fig. 1.1), and daily incubation pattern is negatively associated with sun elevation above the horizon (Fig. 1.6). This pattern, however, does not hold for all *Calidris* species exhibiting reversed sexual size dimorphism. As mentioned previously, this pattern is evident for Least Sandpiper, Baird's Sandpiper and Dunlin (Cramp and Simmons 1983, Miller 1985, Reid and Montgomerie 1985). All three species exhibit reversed sexual size dimorphism to some extent. Nonetheless, there are other monogamous sandpipers that exhibit reversed sexual size dimorphism, but in which females do not incubate predominantly at night (i.e., Semipalmated Sandpiper and Purple Sandpiper; Ashkenazie and Safriel 1979, Pierce 1997, Table 1.2).

Many plover species exhibit the opposite daily pattern of incubation. Female Wilson's Plover, Killdeer (*Charadrius vociferus*), and Kentish Plover (*C. alexandrinus*) are more likely to incubate during the day (Byrkjedal 1985, Bergstrom 1986). Those species do not exhibit sexual size dimorphism; males and females are relatively equal in size (Byrkjedal 1985, Bergstrom 1986, Brunton 1988, Thibault and McNeil 1995). Thus, the pattern of incubation in plovers conflicts with the hypothesis that the pattern of incubation in calidridine sandpipers provides a thermal advantage for females. Body size and potential energetic advantages to incubation during certain parts of the day do not seem to explain satisfactorily why females incubate at night and males incubate during the day. My study, however, does not provide a rigorous test of the differential cost of nocturnal incubation hypothesis. Future studies should examine the metabolic costs of incubating sandpipers and these costs should be evaluated with respect to time of day, sex and structural body size (except see Norton 1973).

Male and female Western Sandpipers had been thought to contribute relatively equal amounts of incubation effort (Erckmann 1981). My study provides direct evidence for male-biased incubation effort and significant temporal difference in incubation effort between sexes. Previous studies investigating the evolution of diversity in avian mating systems have been limited by missing and incorrect information in the literature, resulting in ambiguous assignment of parental roles in their analyses (i.e. Jonsson and Alerstam 1990, Borowik and McLennan 1999). For example, Semipalmated and Western Sandpipers have previously been placed in different parental care categories. Based on results from my study, Western and Semipalmated Sandpipers both exhibit

similar parental care strategies with shared incubation effort and male biased brood care (Chapter 2).

In summary, my study is consistent with the female condition hypothesis, suggesting female energetic reserves may be limited relative to males. This may be attributable to the initially large differences in energetic investment between the sexes. Incubation effort, however, varies among pairs, suggesting additional factors such as individual differences in energy reserves or quality influence incubation pattern. Females incubate at night and accordingly are able to forage during the day when forage availability is presumably greater. Additional study of the diurnal movement of shorebird prey on the breeding grounds is needed to evaluate prey availability. Female *Calidris* species exhibiting reversed sexual size dimorphism typically incubate at night. This may be an indication of a relationship between the costs of nocturnal incubation and body size differences between the sexes. Phylogenetic comparative studies examining reversed sexual size dimorphism and daily pattern of incubation are needed.

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Table 1.1 Pattern of incubation effort over the incubation period for several *Calidris* species with biparental incubation.

Species	Female Incubation Effort	Reference
C. maritima	Decreases	Pierce 1997
C. alpina	Decreases	Soikkeli 1967
C. minutilla	Decreases	Miller 1985
C. pusilla	≈	Ashkenazie and Safriel 1979
C. mauri	Increases	This study

Table 1.2 Daily pattern of incubation and extent of sexual size dimorphism (SSD) for several *Calidris* species with biparental incubation.

Species	SSD	Incubation		Reference
		Daytime	Nighttime	
C. maritima	♀ > ♂	♀ and ♂	♀ and ♂	Pierce 1997
C. alpina	♀ > ♂	♂	♀	Jonsson 1987
C. minutilla	♀ ≈ ♂	♂	♀	Miller 1985
C. mauri	♀ >> ♂	♂	♀	Erckmann 1981
C. pusilla	♀ > ♂	♀ and ♂	♀ and ♂	Ashkenazie and Safriel 1979
C. bairdii	♀ > ♂	♀ and ♂	♀ and ♂	Reid and Montgomerie 1985

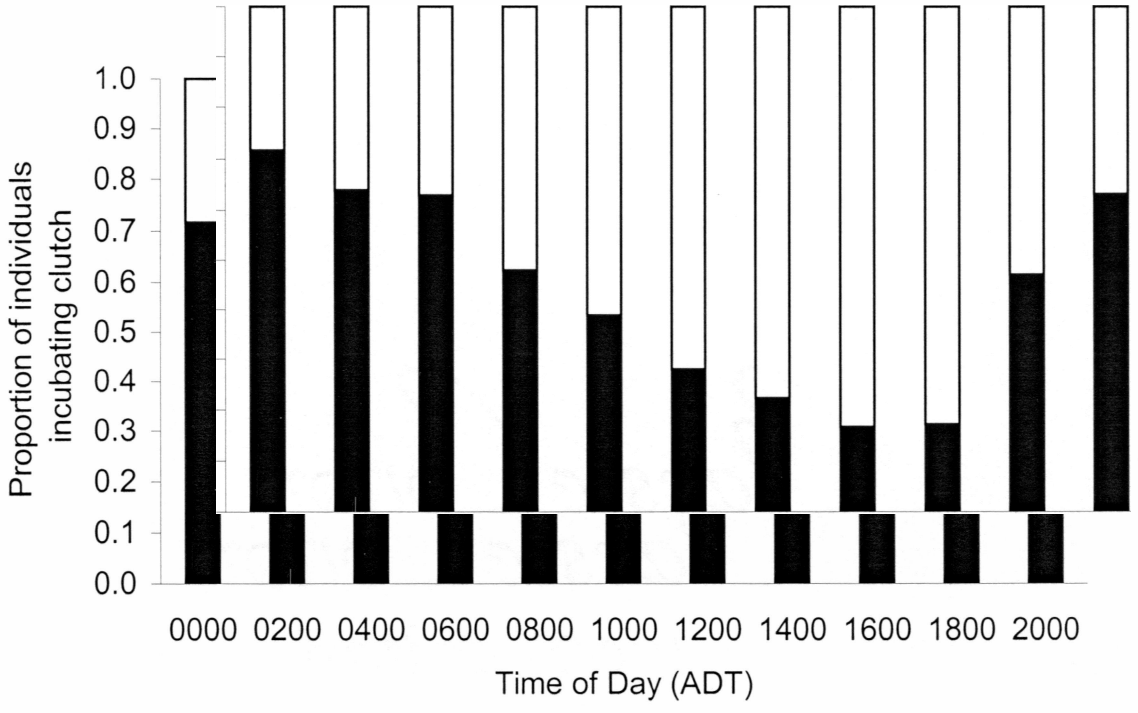


Figure 1.1 Timing of incubation for Western Sandpipers (n = 23) near Nome, AK, during the breeding season, 1999; males (light bars), females (dark bars).

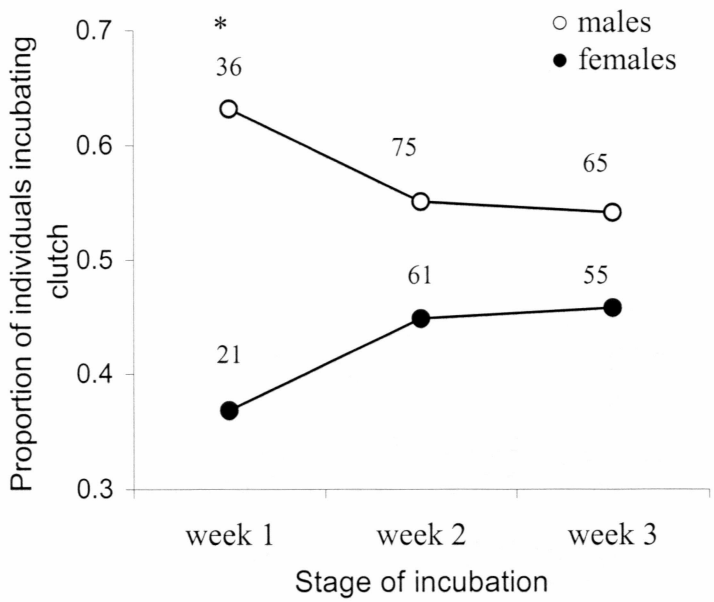


Figure 1.2 The proportion of time male and female Western Sandpipers incubated clutches over the entire incubation period (standardized by clutch initiation date) during the breeding season (28 May-15 July 1999) near Nome, AK (*Binomial test, week 1, $P < 0.05$, $n = 23$ pairs, n is reported for each sex per week).

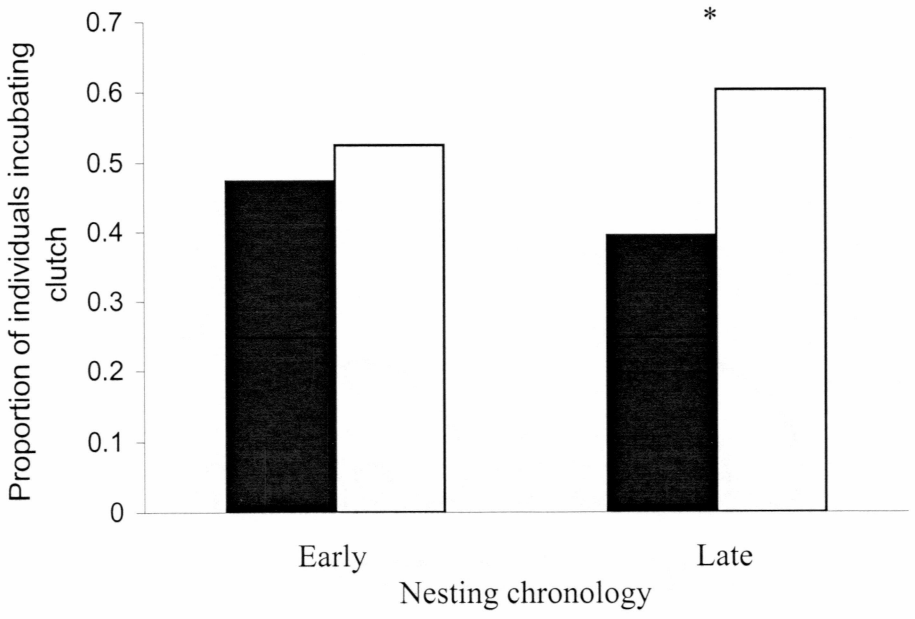
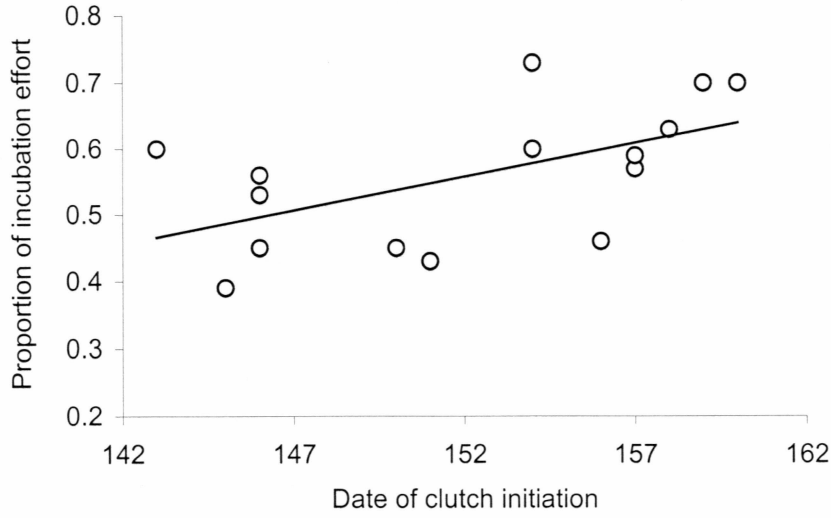


Figure 1.3 The proportion of time early-nesting and late-nesting female (closed bars) and male (open bars) Western Sandpipers incubated clutches near Nome, AK. Early nesters were defined as pairs that initiated nesting before the median nest initiation date (*t test, $t = 2.25$, $P = 0.04$, $n = 13$ pairs).

(a)



(b)

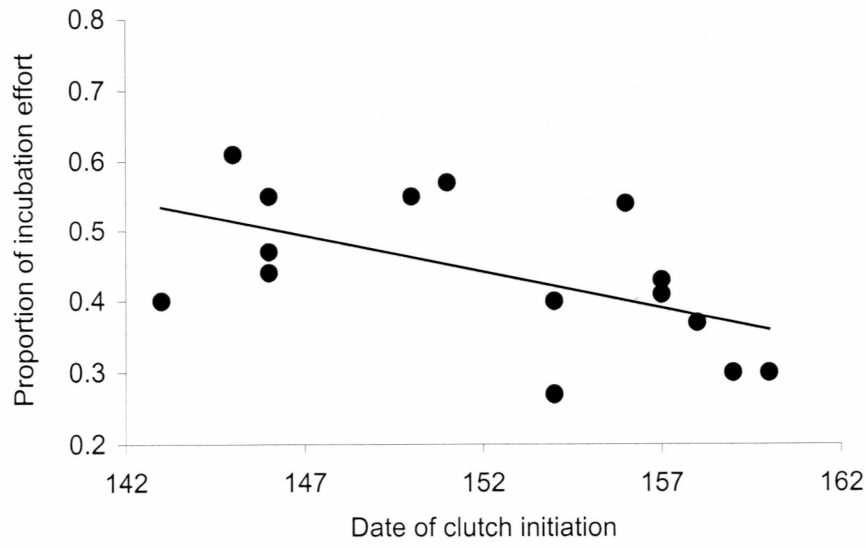


Figure 1.4 The proportion of time male (a) and female (b) Western Sandpipers incubated clutches, as a function of clutch initiation date near Nome, AK, ($R^2 = 0.25$, $P = 0.06$, $n = 15$).

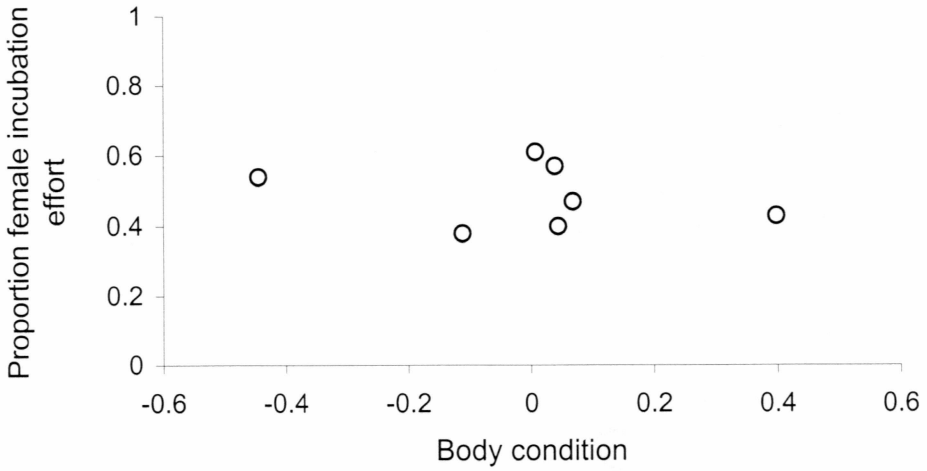


Figure 1.5 Proportion of total incubation effort as a function of body condition during incubation for female Western Sandpipers nesting near Nome, AK, 1999 ($F_{2,6} = 0.97$, $P = 0.4$, $n = 7$).

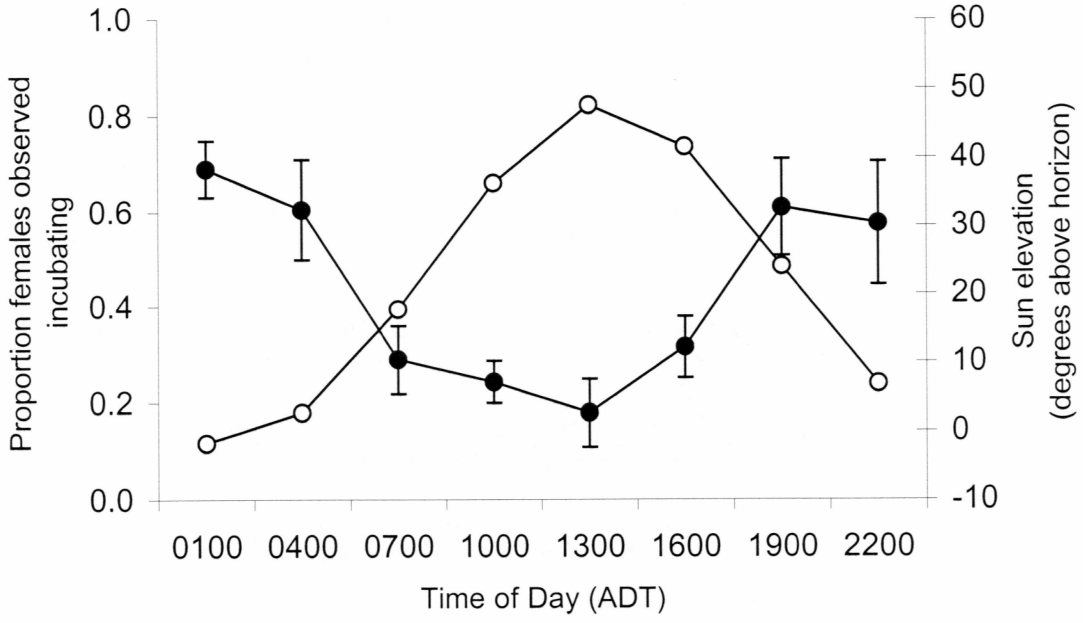


Figure 1.6 The proportion of time female Western Sandpipers incubated clutches (standardized by clutch initiation date) as a function of time of day near Nome, AK, (●); error bars show standard deviations in the proportion incubating during 3-week incubation period. Open circles (○) represent mean elevation of the sun (degrees above horizon) for June 1999, as a function of time of day.

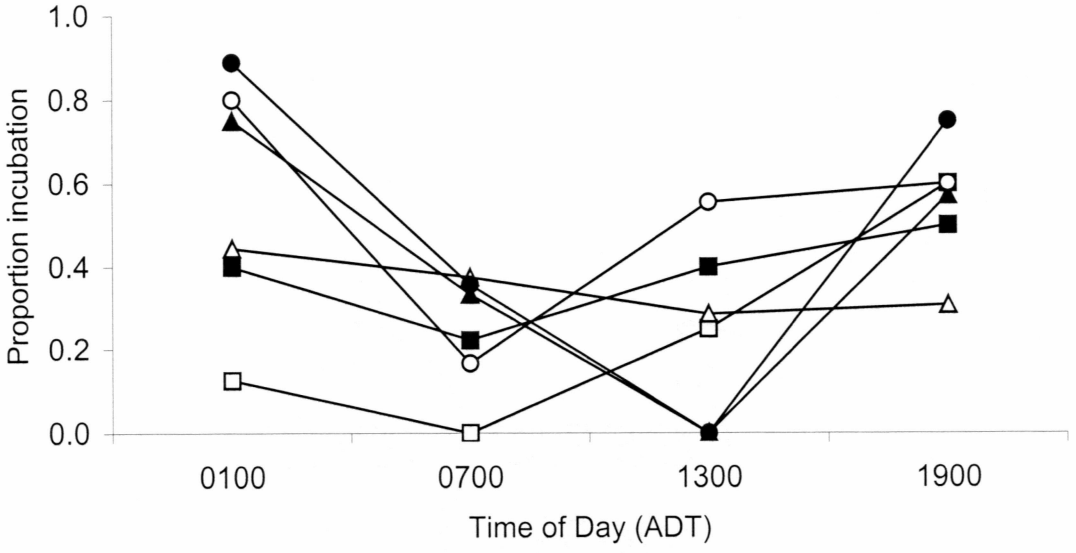


Figure 1.7 Timing of incubation for six female Western Sandpipers near Nome, AK, during the breeding season, 1999.

CHAPTER 2. DETERMINANTS OF BROOD DESERTION IN THE MONOGAMOUS WESTERN SANDPIPER[2]

Abstract. Parental desertion of offspring before independence is common among birds, but not well understood. Among shorebirds, females are more likely to desert than males. Three hypotheses propose to explain female brood desertion: (1) energetic limitation, (2) increased female survival, and (3) remating opportunity. I investigated male and female Western Sandpiper (*Calidris mauri*) contribution to parental care during the breeding season near Nome, AK (64° N) during 1998 and 1999. I repeatedly observed which parent tended the brood during the brood care period. Males remained with broods more often and longer than did females. Females deserted their broods an average of 5.6 days after hatch, while males tended broods an average of 13.0 days after hatch ($P < 0.001$). Nests that hatched earlier in the season received significantly more bi-parental care during the brood care period ($P = 0.01$). None of the three hypotheses satisfactorily explains why female Western Sandpipers desert broods early.

Key words: Brood care, *Calidris mauri*, mate desertion, parental care, parental roles, Western Sandpiper.

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[2] Prepared for submission in Condor.

INTRODUCTION

Optional uniparental brood desertion by either parent following hatch is common among shorebirds (Ashkenazie and Safriel 1979, Gratto-Trevor 1991, Miller 1985, Pierce 1997). Desertion is defined here as the termination of care by one parent before the young are independent (Kelly and Kennedy 1993). For most *Calidris* species, the female is more likely than the male to desert the brood shortly after hatch. The evolution of this behavioral trait is often explained by the costs and benefits of current and future reproductive attempts (Maynard Smith 1977), which vary depending on several ecological factors (i.e. weather, predators). Selection for parental care during brood-rearing seems likely because the main benefit of parental care is an increase in chick survival (Szekely and Cuthill 1999, Amat et al. 2000). Nonetheless, continued care imposes fitness costs for parents, such as increased risk of predation (Byrkjedal 1985, Szekely and Cuthill 2000).

To explain parental desertion, one must consider the trade-off between increasing survival of young until fledging vs. increasing parent survival and future reproductive success. The costs and benefits of desertion must be considered separately for each parental sex because costs and benefits likely vary between the sexes. In addition, costs and benefits probably vary temporally during the period of parental care. Temporal variation in the costs and benefits of desertion and differences between sexes, could lead to a conflict of interest between parents (Gross and Sargent 1985).

The reasons for female desertion among monogamous bird species are not clearly understood, and evidence for costs and benefits to either sex is scant (Clutton-Brock

1991). Several hypotheses have been formulated to account for offspring desertion. Some of these relate specifically to shorebirds because these birds exhibit an exceptional diversity of mating and parental behavioral traits, making shorebirds excellent subjects to investigate adaptive explanations for parental care patterns (Erckmann 1983, Szekely 1996, Amat et al. 1999). These hypotheses include: (1) energetic limitation imposed on breeding females by the costs of reproduction (differential parental capacity; Ashkenazie and Safriel 1979, Erckmann 1981, Pierce 1997); (2) increased female survival (Ashkenazie and Safriel 1979, Gratto-Trevor 1991); and (3) increased opportunity to acquire new matings within the same breeding season (remating opportunity hypothesis; Szekely et al. 1999).

Erckmann (1981) proposed the differential parental capacity hypothesis to explain early brood desertion in female shorebirds. The hypothesis states that egg laying may not reduce female energy reserves to the point that they cannot incubate, but because of egg-laying costs, females are energetically constrained and thus less able to assume brood care duties. Considerable evidence exists for decreased female condition during the breeding season, relative to males (reviewed in Chapter 1). Body weight is commonly used as an indicator of female condition (Gratto-Trevor 1991), and weight loss has been documented for females in several shorebird species during the breeding season (Ashkenazie and Safriel 1979, Erckmann 1981, Brunton 1988, Gratto-Trevor 1991).

Limited energy reserves during brood rearing may be a direct consequence of the costs incurred by egg laying (Clutton-Brock 1991, Pierce 1997). This is thought to be particularly important for female shorebirds because they lay large eggs in relation to

their body size (Rahn et al. 1975). Pierce (1997) proposed female desertion may benefit both sexes if egg size or quality is maximized (Pierce 1997). Egg laying has been shown to cause initially large differences in energetic investment between the sexes in Semipalmated Sandpipers (*Calidris pusilla*) (Ashkenazie and Safriel 1979). Previous examination of the differential parental capacity hypothesis resulted in conflicting evidence, thus warranting additional evaluation (Erckmann 1981, Amat et al. 2000).

Myers (1981) suggested female desertion may increase female survival by allowing early migration. In other words, females may restrain themselves from providing brood care to increase lifetime reproductive success. Most studies of *Calidris* species reported brood desertion was strongly dependent on hatching date (Gratto-Trevor 1991, Szekely and Cuthill 1999, Amat et al. 2000, Currie et al. 2001); parental desertion was earliest in the rearing period for late-hatching clutches. Early hatch and brood desertion by both parents may allow for early departure to wintering grounds. Myers' (1981) hypothesis clearly predicts that timing of migration is important for increased survival. Delay of departure on southbound migration may be so costly that females limit brood care and potentially current brood success to increase annual survival and lifetime reproductive success. Because migration costs likely increase with increasing migration distance, individuals migrating longer distances may be more constrained than individuals breeding at lower latitudes in the amount of time they can remain on territory (Currie et al. 2001). Furthermore, differences in migration costs likely cause some shift in the costs and benefits of brood attendance. If early migration provides some benefit to

the attending parents, it may come at the cost of decreased reproductive success caused by early brood desertion.

The differential parental capacity and increased female survival hypotheses are not mutually exclusive. The mechanisms influencing timing of female desertion predicted by each hypothesis, however, are independent. The differential parental capacity hypothesis states female energetic limitation constrains female brood care, whereas the increased female survival hypothesis implies females are restraining themselves from providing brood care to increase lifetime reproductive success. These two competing hypotheses will be referred to as the energetic constraint (Differential parental capacity, Erckmann 1981) and female restraint (Increased female survival, Ashkenazie and Safriel 1979) hypotheses.

The remating opportunity hypothesis suggests a parent deserts its offspring to remate, thus increasing individual reproductive success (Oring 1986, Szekely and Williams 1995). Under this hypothesis, the decision to desert is governed by the trade-off between the value of the current breeding event vs. future breeding prospects (Clutton-Brock 1991). If individuals are capable of remating within a season, the costs of terminating care for the first brood may be outweighed by the benefits of producing a second brood. To explain female desertion, Szekely and Cuthill (2000) suggested females gained greater increase in reproductive success by deserting than did males, and this was a direct function of the operational sex ratio. Availability of suitable mates is thought to be strongly associated with benefits of brood desertion (Szekely and Cuthill 2000). This hypothesis is well supported for those species exhibiting multiple nesting

attempts within a season (i.e Kentish Plover *Charadrius alexandrinus*; Szekely and Cuthill 2000). To date, little evidence has been reported for remating in *Calidris* species (except see Soikkeli 1967). Thus, the remating opportunity hypothesis does not explain female brood desertion for Western Sandpipers or any of the single clutch arctic nesting *Calidris* species.

In this study, I investigated brood desertion in Western Sandpipers (*Calidris mauri*), a monogamous shorebird with shared brood care (Holmes 1971), and early offspring desertion by females (Erckmann 1981). Western Sandpiper chicks are precocial, leave the nest within 24 hr of hatching, and are never fed by their parents (Holmes 1972). I had three objectives: (1) to quantify the timing of offspring desertion by females; (2) to examine factors associated with timing of female desertion in an evolutionary context; and (3) to use these data to evaluate the following two hypotheses proposed to explain female brood desertion.

Hypothesis 1: energetic constraint. Females are energetically limited because of the costs of egg production and, consequently, provide limited brood care (Erckmann 1981, Pierce 1997). **Prediction 1-A**. If females terminate brood care early as a result of reduced energy reserves, then timing of brood desertion should be a function of female body condition. Assuming energy reserves and body condition are related: **Prediction 1-B**. If reduced female energy reserves are a result of egg quality or size, there will be an inverse relationship between brood attendance and egg size after adjusting for body size and hatch date.

Hypothesis 2: female restraint. Early brood desertion increases female survival through early migration (Myers 1981). Timing of departure from the breeding site may be restrained to increase annual survival and lifetime reproductive success. **Prediction 2-A**. If timing of departure for south-bound migration limits brood attendance, late-nesting females may be more constrained and thus attend broods for fewer days than early nesting females. **Prediction 2-B**. If early nest initiation results in earlier departure for south-bound migration, then return rates will be higher for early nesting vs. late-nesting females. **Prediction 2-C**. If females limit brood care in response to early departure for migration, then timing of brood desertion will vary directly with migration distance. **Prediction 2-D**. If early female brood desertion decreases brood survival, then female brood care and timing of migration will vary directly with annual offspring return rates.

METHODS

STUDY AREA

I studied the division of parental roles in Western Sandpipers near Cape Nome (64°20'N, 164°56'W) on the southwest tip of the Seward Peninsula, 21 km east of Nome, AK from May to July 1998 and 1999. The 4 km^2 study area, located on the western edge of Safety Sound, consisted of a mosaic of low ridges and tundra ponds (Sandercock 1998a). The breeding biology of this population of Western Sandpipers has been studied since 1993 (Sandercock 1998a).

FIELD METHODS

I located nests by systematically walking the tundra and observing sandpipers that flushed or gave distraction displays (Sandercock 1998a). If I could not find the clutch immediately after the parent flushed, I observed the bird from 20 to 25 m until it returned to the nest. Nests were marked with a line of sticks (4) and a short stake placed 10 m from the nest cup. I captured incubating birds using traps placed over the nest. Captured adults were given unique color band combinations and numbered metal bands. I attempted to capture both parents attending a nest. Exposed culmen length, tarsus length, and flattened wing chord were measured to the nearest 0.1 mm. Sex was determined using culmen length (<24.2 mm for male, >24.8 mm for female; Cartar 1984) and mating behavior. No overlap in culmen length between males and females reduced the likelihood of misclassifying sex of an individual. I weighed adults with a Pesola balance (± 0.5 g). An index of body condition was obtained as the residuals from a multiple regression of body mass on a measure of structural body size and number of days after clutch completion that mass was measured. Structural body size was estimated using principal component analysis. Body condition estimates were based on post-clutch completion measurements of body mass. For each egg in a clutch, I measured egg width and breadth using vernier calipers (± 0.1 mm). Egg volume index was estimated by the product of egg width x breadth^2 (Hoyt 1979) If a nest already contained four eggs when located, egg buoyancy was used to estimate stage of incubation (Sandercock 1998b). Otherwise, clutch initiation and completion of laying were determined from egg laying schedules based on previous observation of the mean length of incubation for Western Sandpipers (Sandercock 1998b). Nests were monitored until they failed (predation,

desertion) or successfully fledged chicks. A successful nesting attempt was defined as having at least one chick hatch. Data were collected in accordance with Institutional Animal Care and Use Committee guidelines at the University of Alaska Fairbanks.

Nests were checked on a regular basis (every 3-5 days), and then daily as the clutch approached hatching. Within 12 hr of hatch, nestlings were banded with numbered metal bands. Broods (n=24) were located daily and occasionally twice a day. I approached previously known locations of broods and surveyed the area until I located the brood, recording its location on a schematic diagram of the study site. I then remained in the area for up to 15 minutes to determine if both the male and female were attending the brood. If a parent was absent for three consecutive days, then I assumed that parent deserted on the first day it was recorded as absent. Data collected from 1994 to 1997 (Sandercock pers.comm.) at the Cape Nome study site was used to determine return rates of adult females. Successful resights were defined as an observation of a nesting adult female (color banded and nest trapped) in the following year of a previous year's nesting attempt. If an adult was observed in multiple years (n = 5), these observations were excluded from analyses.

STATISTICAL ANALYSES

I used principal component analysis to create an index of Western Sandpiper body size based on culmen and wing length using a correlation matrix (Rising and Somers 1989). Loadings for culmen and wing chord were positive in the first principal component and this component explained 69.0% of the variation in body size. I used a two-sample t-test to determine if mean number of days females provided brood care varied by year. I used

an analysis of covariance (ANCOVA) to test for a difference between the sexes in timing of desertion as a function of year in which year was the factor and number of days parent remained with the brood was the covariate. I used stepwise multiple linear regression to determine the relationship between the number of days each parent remained with the brood and hatch date, egg volume index, female body size and female body condition (SAS Institute, 2000). Standardized and partial regression coefficients are provided to help with interpretation of multiple regression results. Exploratory multiple regression indicated female body condition during incubation did not explain variation in female brood care, in part because it is correlated with egg volume ($P = 0.06$). Examining the correlation matrix for all variables included in the multiple regression indicated female body condition during incubation and timing of brood desertion were not significantly correlated ($P = 0.9$). Timing of desertion was analyzed by an ANCOVA in which parental sex was the factor and hatch date was the covariate (Zar 1996). Normal approximation to the binomial was used to determine if early nesting females were more likely to return the following year than late nesting females. All observations between years were made on unique individuals, except in one case, where a female from 1998 remated with a different male in 1999. All data were inspected for normality and homoscedasticity (Zar 1996). In all analyses, probability of committing a Type I error was set to $\alpha = 0.05$.

RESULTS

A combined total of 24 Western Sandpiper broods in 1998 and 1999 was monitored to determine timing of brood desertion. Females deserted broods before their mates in 22 of 24 cases (91.6%). The mean number of days both parents cared for their brood did not vary between years ($t = 1.125$, $P > 0.05$, $n = 22$). Mean (±SD) female care was 5.6 (± 2.5) days (range 2 - 11, Table 2.1). Mean hatching date was similar in 1998 and 1999 (25 June, $F_{1,21} = 0.15$, $P = 0.7$, Table 2.1).

It was difficult to determine when the second parent deserted because chicks were less visible when protective parents were absent. For some broods ($n = 3$), chicks were seen alone before fledging. For most broods ($n = 16$), chicks were observed until fledging. Mean (±SD) duration the remaining parent cared for the brood was 13.0 (± 4.5) days (range 6 - 21). The second parent deserted the brood on average 7.0 days following desertion by the first parent.

ENERGETIC CONSTRAINT

A multiple regression of body condition, body size, egg volume, hatch date, and number of days females remained with their broods indicated that hatch date explained a substantial portion of the variation in female brood desertion (multiple $R^2 = 0.64$, Table 2.2, Fig.2.1a). **Result 1-A**. This analysis detected a significant effect of body size and egg volume (Table 2.2), but not of body condition. Results of the multiple regression indicate early-nesting pairs provided more brood care (Fig. 2.1a,b), and large females provided more care than small females (Table 2.2). **Result 1-B**. Number of days females remained with their broods was negatively associated with egg volume (Table 2.2). Females that produced larger eggs remained with the brood for fewer days than females

that produced smaller eggs after controlling for hatch date, body size and body condition. A positive correlation was found between egg volume and female body condition during incubation ($r = 0.57$, $P = 0.06$, Fig. 2.2). Examining simple correlation coefficients indicated no association between body condition during incubation and timing of female brood desertion ($r = -0.049$, $P = 0.9$). Male brood care was not associated with mean egg volume ($b = -0.602$, $t = -0.11$ $P = 0.9$, $n = 18$).

FEMALE RESTRAINT

Result 2-A. Nests that hatched earlier in the season received significantly longer bi-parental care during the brood care period (b = - 0.256, $t = -3.72$ $P = 0.01$, $n = 18$). Early-hatching nests received longer care by both parental sexes (Fig. 2.1a,b). A significant effect of parental sex was found for brood attendance ($F_{3,31} = 12.61$, $P = 0.001$); males provided significantly more care and the duration of male care decreased more rapidly with respect to hatch date than female care ($t_{31} = 2.97$, $P < 0.05$ Fig. 2.3b). Adults initiating nests early left the site earlier than late nesters (b = - 0.426, $t = -5.07$ $P < 0.001$, $n = 18$, Fig. 2.3a). **Result 2-B**. Adult female survival in relation to median hatch date indicated females with early hatch dates were more likely to return the following year (z = 2.3389, $P < 0.05$, Fig. 2.4). Based on plumage examinations at the time of banding (O'hara MS), I assumed that most females breeding at this site were adults (>2 yrs old) and not first-year breeders (Sandercock 1998a).

It was difficult to address brood survival because return rates are usually very low for Western Sandpipers (Sandercock 1998a). Of 200 chicks banded at the study site between 1993 and 1998, 14 were observed in a following season. **Result 2-C**. Early-

hatching clutches produced 6 of these chicks, while clutches hatching on or later than the median hatch date produced the remaining 8.

DISCUSSION

The decision to desert from brood care varies with timing of hatch, as early-nesting females provided longer brood care (Fig. 2.1a). A similar pattern has been observed in other species (i.e. Dunlin, Soikkeli 1967; Semipalmated Sandpiper, Ashkenazie and Safriel 1979; Least Sandpiper, Miller 1985; Gratto-Trevor 1991; Kentish Plover, Szekely and Williams 1995; Eurasian Curlew, Currie et al. 2001). Likewise, male Western Sandpipers remained with earlier-hatching broods longer than those with later-hatching broods, indicating that males may face similar constraints as females (Fig. 2.1b). Below, I compare my data to hypotheses proposed to explain this tradeoff.

ENERGETIC CONSTRAINT

Erckmann (1981) suggested female brood desertion results from energetic limitations imposed on breeding females by the costs of egg production and incubation. Under this hypothesis, a female deserts her brood because she is in poor body condition. My data indicate that for Western Sandpipers, it seems unlikely that poor body condition directly causes females to desert their brood, as body condition during incubation was not a significant indicator of brood desertion (Table 2.2). Nonetheless, body condition was positively correlated with egg volume. It is important to note that my estimate of female body condition may be slightly skewed towards smaller birds, as larger individuals may have absolutely more body fat than is expected from an increase in structural size. My

data also indicated females may trade off the benefit of brood care against the benefit of maximizing egg size. By statistically controlling for hatch date body size and body condition, I found timing of brood desertion was partially explained by egg volume, suggesting female investment early in the season limited brood care (Table 2.2).

Amat et al. (2000) examined the role of energetic costs in offspring desertion by the Kentish Plover through experimentally lengthening or shortening the duration of incubation by one week. No differences in the timing of brood desertion between experimental and control females were found, indicating energetic costs did not explain offspring desertion. Furthermore, the timing of brood desertion by females was not affected by their body condition. Although body condition did not directly explain timing of brood desertion in female Western Sandpipers, it was positively correlated with egg volume, suggesting body condition may be indirectly related to timing of brood desertion. The direction of this relationship, however, is the reverse of what was expected. Females that laid large eggs were in good condition during incubation and females that laid large eggs provided less brood care. My estimates of body condition were based on post-clutch completion body mass, thus females either arrive on the breeding site in good condition or are able to acquire the energy required to produce large eggs, without negatively influencing body condition after clutch completion. My data may provide partial support for the energetic constraint hypothesis. Perhaps females provide an energetic investment either early by laying larger eggs or later by providing longer brood care.

FEMALE RESTRAINT

A benefit of early brood desertion may be early migration and increased survival (Myers 1981, Gratto-Trevor 1991, Currie et al. 2001). My results indicate that for Western Sandpipers, early nest initiators provided more brood care (Fig. 2.1), and were more likely to return the following season (Fig. 2.4), suggesting female parents benefit from early nest initiation. I did not find that chicks from early hatching clutches were more likely to return the following season, although statistical power was low. Both the study site and surrounding area (± 5 km) where searched on a regular basis. Parents initiating nests early not only provided more brood care but also departed the area earlier (i.e. early migration, Fig. 2.3a), though this relationship is likely to be highly dependent on female age.

My data indicated length of brood care and the association between brood care and hatch date are significantly different for males and females. Males provided more care; however, the amount of care decreases more rapidly with respect to hatch date (Fig 2.3b). The differences between male and female care in relation to hatch date indicate a threshold date whereupon adults, regardless of sex, desert broods and begin south-bound migration (Fig 2.3a). Individuals of both sexes nesting early in the season provided longer brood care, departed the study site earlier, and early-nesting females are likely to return in the following year (Fig. 2.4). This suggests strong directional selection for traits associated with early nest initiation; however, there is considerable variation associated with both timing of nest initiation and duration of brood care within this population. Costs associated with early arrival and the persistence of low quality individuals in the population due to environmental stochasticity may maintain this variability.

Until recently, few data were available to evaluate the optimal timing of migration to the wintering grounds as an explanation for timing of female desertion (Myers 1981, Gratto-Trevor 1991, but see Currie et al. 2001). This hypothesis assumes longer migration distance increases the costs of migration. Currie et al. (2001) provided preliminary supporting evidence in the form of a latitudinal gradient in the timing of brood desertion in the Eurasian Curlew. Individuals in northern populations appeared to be more constrained in the amount of time they can remain on the breeding territory than those individuals breeding at lower latitudes. Female desertion varies inversely with both hatching date and migration distance (Currie et al. 2001). For Western Sandpipers breeding at Nome, AK (64° N), females deserted broods 5.6 ± 0.53 ($\bar{x}$ ± SE) days post hatch (n = 22). Ruthraugh (unpubl. data) reported female Western Sandpipers breeding at Kanaryaraq, AK (61° N) deserted broods 7.2 ± 0.61 ($\bar{x}$ ± SE) days post hatch (n = 48). Females breeding at Nome, AK remained with broods for significantly fewer days than females breeding further south (t = 11.17, $P < 0.001$). Brood desertion data from these two breeding sites are suggestive of a relationship between latitude and migration distance for Western Sandpipers.

Differences in duration of brood care between the sexes for Western Sandpipers may be related to relative migration distances. Unpublished data indicate there is significant sexual segregation for adult Western Sandpipers on the wintering grounds (Nebel et al. MS.). Females overwinter further south, thus costs of migration may be higher than those of males. In addition, males are likely less constrained than females with timing of migration. Timing of migration may relate to timing of wing moult (Nebel

et al. MS.). Early arrival on the wintering grounds allows for complete wing moult before arrival of predators (Ydenberg, Butler, Lank and Ireland, pers. comm.). If early migration and early wing moult increase adult survival, it is likely that timing of brood desertion is important for both sexes. This is supported by the fact that parental care provided by males and females becomes more constrained in later-hatching broods. Differences in timing of brood desertion between the sexes may be a direct consequence of differential migration.

In conclusion, I found partial support for the energetic constraint hypothesis. Female body condition during incubation did not vary with timing of brood desertion, although females in good body condition laid larger eggs. Females that laid large eggs provided less brood care, indicating a tradeoff between egg size or quality and brood care. Variation in timing of female brood desertion may be in response to initially large differences in energetic investment in egg size or quality. My data indicate an indirect association between body condition and brood care, however, this association is in contrast to the prediction that females are energetically constrained and thus are unable to provide brood care.

A benefit of early brood desertion may indeed be early migration and increased survival. That parents with early hatching broods provided more care and departed the breeding site early provides compelling evidence that timing of brood desertion is related to cross-seasonal factors, such as timing of south-bound migration. Whether variation in timing of brood desertion between the sexes may be explained by differential migration is unknown and deserves additional study.

My data support the hypothesis that individuals may gain from early departure; however, the two hypotheses reviewed here are not mutually exclusive. Both energetic constraints and increased lifetime reproductive success likely influence strategies and decisions at the breeding grounds. This is a good example of the need for multiple hypotheses to explain complex behaviors. Whether variation in timing of brood desertion is more strongly associated with energetic constraint or increased female survival is difficult to determine and deserves additional study.

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Table 2.1 Length of time Western Sandpiper parents spent with broods near Nome, AK, 1998 and 1999. For date, June 1 = 152. Day 1 = day clutch hatched.

Year	Number of broods	Mean hatch date (s.d.)	Mean no. days before female deserted (s.d.), range	Mean no. days before male deserted (s.d.), range
1998	12	176.0 (4.94)	6.0 (2.80), 2 - 11	13.0 (3.38), 8 - 18
1999	12	176.5 (5.82)	4.9 (1.91), 2 - 9	13.0 (4.94), 7 - 21

Table 2.2 Multiple-regression statistics for an examination of the effects of egg volume, hatch date and body size on the number of days female Western Sandpipers remained with broods near Nome, AK, during 1998 and 1999. $n = 22$ females.

	Standardized regression coefficient	Partial regression coefficient	t	P
Hatch date	-0.648	0.327	-3.72	0.004
Egg volume	-0.513	0.279	-2.93	0.015
Body Size	0.445	0.387	2.52	0.031

Notes: $R^2 = 0.703$, adjusted $R^2 = 0.614$; P values reflect a two-tailed test.

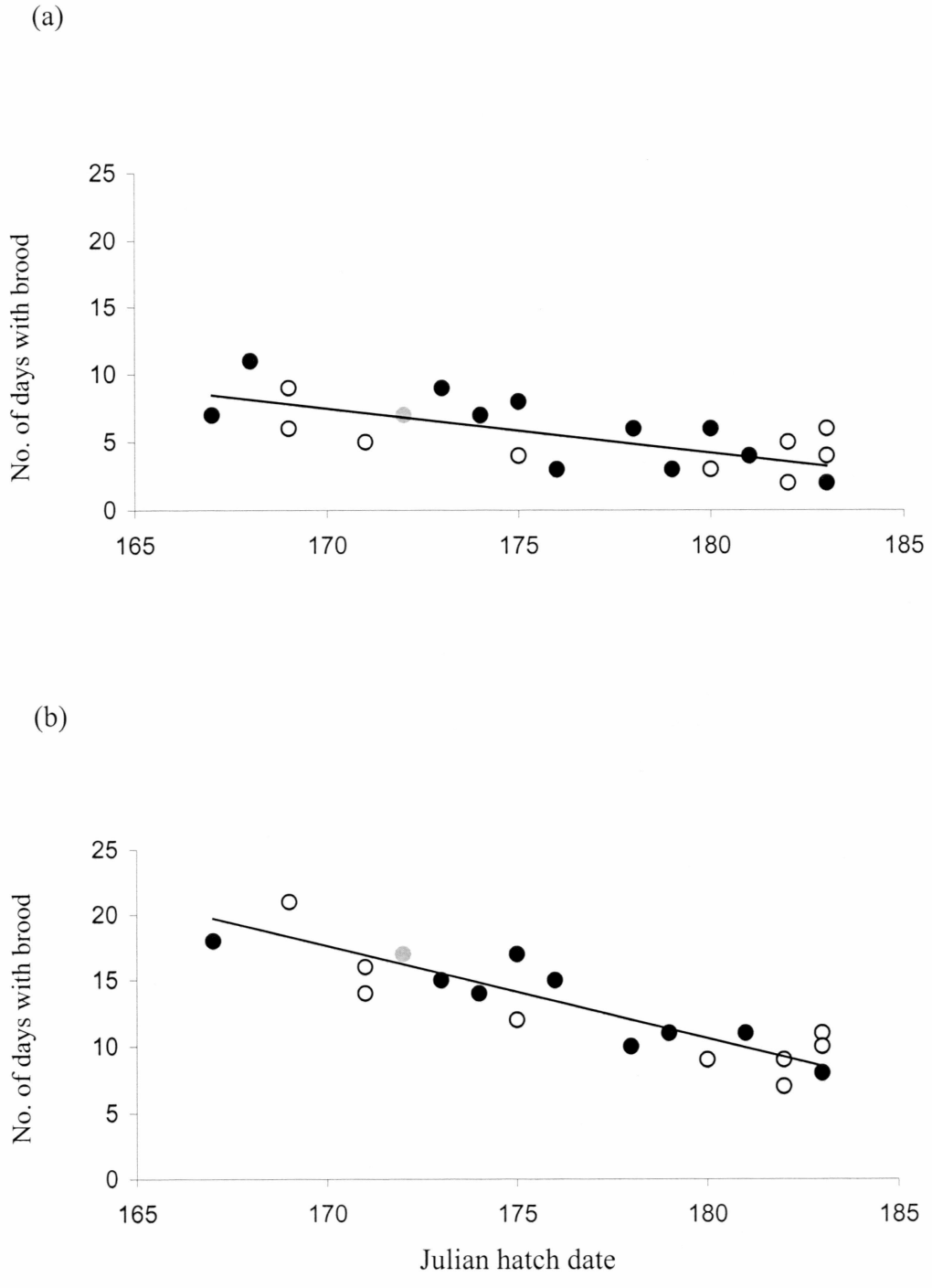


Figure 2.1 Timing of brood desertion relative to hatch date in (a) female ($P = 0.01$) and (b) male ($P < 0.001$)Western Sandpipers nesting near Nome, AK. Each dot represents a brood (● 1998; ○ 1999). The gray dot represents brood deserted by male before female.

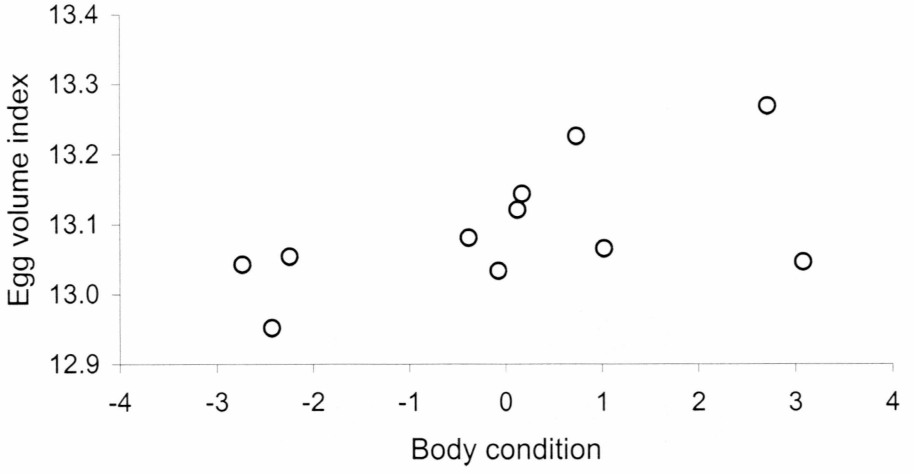
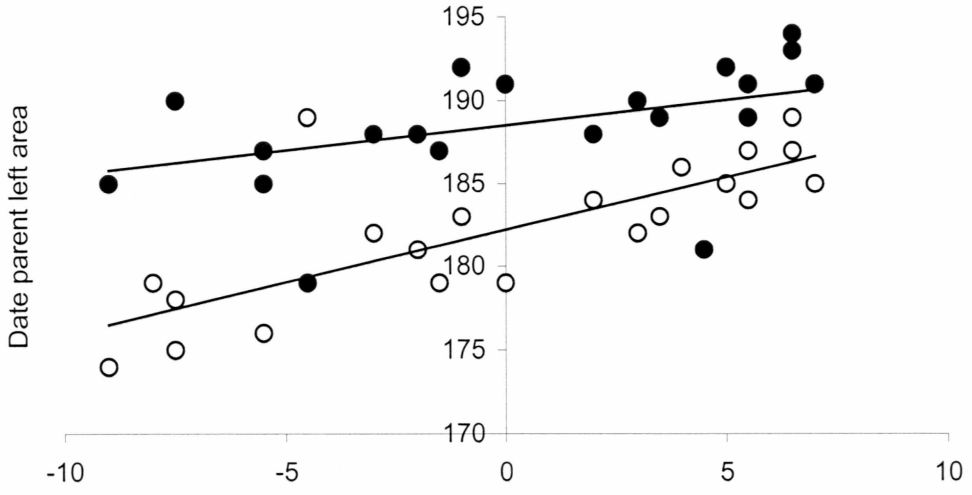


Figure 2.2 Mean egg volume as a function of female body condition for female Western Sandpipers nesting near Nome, AK, in 1998 and 1999 ($r = 0.568$, $P = 0.06$, $n = 11$).

(a)



(b)

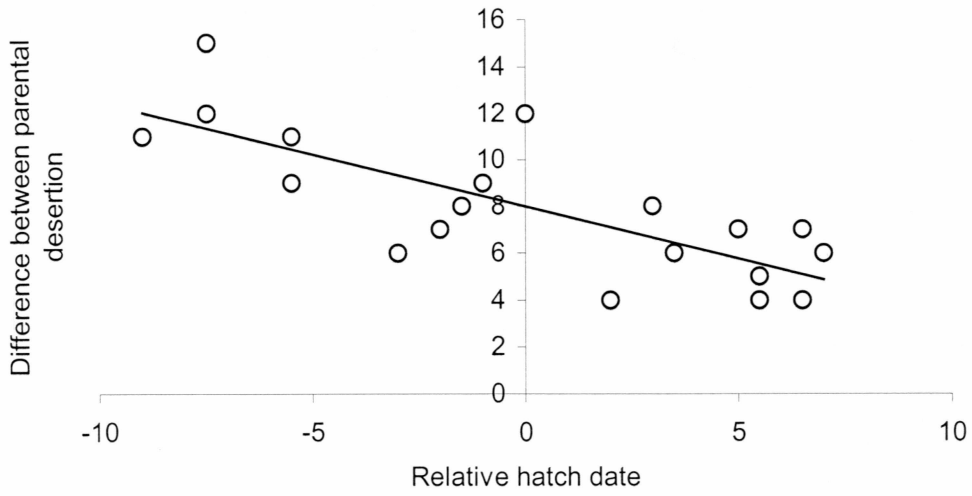


Figure 2.3 (a) Date parent (○ female, • male) left the study site as a function of relative hatch date (hatch date – mean hatch date). (b) Difference in the number of days between parental desertion as a function of relative hatch date for Western Sandpipers nesting near Nome, AK, in 1998 and 1999 ($R^2 = 0.59$, $P<0.001$, $n = 19$).

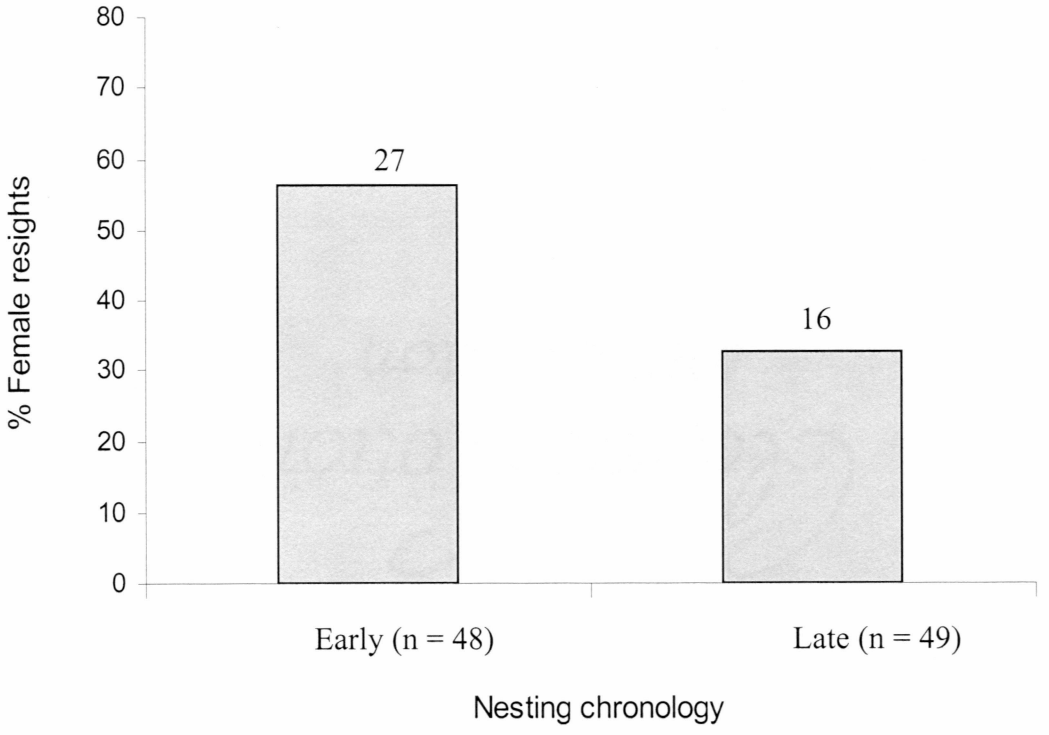


Figure 2.4 Proportion of returning adult female Western Sandpipers relative to hatch date nesting near Nome, AK, (binomial test z = 2.3389, $P<0.05$). Early nesting females are defined as females that initiated nests before the median nest initiation date.

SUMMARY

In chapter I, I examined two hypotheses explaining division of incubation effort in Western Sandpipers. The female condition hypothesis states females may recover energy spent on eggs most efficiently if males incubate when food is most available, allowing females to feed at those times. My data are consistent with the female condition hypothesis, suggesting female energetic reserves may be limited relative to males. This may be attributable to the initially large differences in energetic investment between the sexes. Incubation effort, however, varies among pairs, suggesting additional factors such as individual quality influence incubation pattern. Females incubate at night and accordingly are able to forage during the day when forage availability is presumably greater. Additional study of the diurnal movement of shorebird prey on the breeding grounds is needed to evaluate prey availability.

The differential cost of nocturnal incubation hypothesis states temporal differences in incubation duties between the sexes yield unequal effort per unit time. Body size and potential energetic advantages to incubation during certain parts of the day do not seem to explain satisfactorily why females incubate at night and males incubate during the day. My study, however, does not provide a rigorous test of the differential cost of nocturnal incubation hypothesis. Future studies should examine the metabolic costs of incubating sandpipers and these costs should be evaluated with respect to time of day, sex and structural body size.

In chapter II, I quantified the timing of offspring desertion by female Western Sandpipers and examined factors associated with timing of female desertion in an

evolutionary context by evaluating two hypotheses proposed to explain female brood desertion. The energetic constraint hypothesis states females are energetically limited because of the costs of egg production and, as a consequence, provide limited brood care. I found partial support for the energetic constraint hypothesis. Timing of female brood desertion did not vary with body condition during incubation, although females that laid larger eggs were in good body condition. Energetic limitation may influence timing of female parental investment. Females provided an energetic investment either early by laying larger eggs or later by providing longer brood care. Thus, variation in timing of female brood desertion may be in response to initially large differences in energetic investment in egg size or quality.

The female restraint hypothesis states early brood desertion increases female survival through early migration. Timing of departure from the breeding site may be restrained to increase annual survival and lifetime reproductive success. A benefit of early brood desertion may indeed be early migration and increased survival for Western Sandpipers. That parents with early hatching broods provided more care and departed the breeding site early provides compelling evidence that timing of brood desertion is related to cross-seasonal factors, such as timing of south-bound migration. Whether variation in timing of brood desertion between the sexes may be explained by differential migration is unknown and deserves additional study. Both energetic constraints and increased lifetime reproductive success likely influence strategies and decisions at the breeding grounds. Whether variation in timing of brood desertion is more strongly

associated with energetic constraint or increased female survival is difficult to determine and deserves additional study.

Male and female Western Sandpipers had been thought to contribute relatively equal amounts of incubation and brood care effort. My study provides direct evidence for male-biased parental care and strong seasonal declines in female incubation effort and brood attendance. Reduced parental care by both sexes late in the season may be in response to time constraints associated with seasonal environments. Cross-seasonal behaviors have been shown to vary between the sexes (i.e. duration of brood care; migration distance; over-wintering forage behavior) and thus should be considered to generate and test hypotheses attempting to explain parental care strategies and mating system evolution for Western Sandpipers.